

## BIOLOGY AND COMPARATIVE ANATOMY OF THREE NEW SPECIES OF COMMENSAL GALEOMMATIDAE, WITH A POSSIBLE CASE OF MATING BEHAVIOR IN BIVALVES

Paula M. Mikkelsen<sup>1</sup> & Rüdiger Bieler<sup>2</sup>

### ABSTRACT

Three new galeommatid bivalves, *Divariscintilla octotentaculata*, *D. luteocrinita*, and *D. cordiformis*, are described as commensals occupying the burrows of the mantis shrimp *Lysiosquilla scabricauda* from central eastern Florida. Morphological comparisons are made with all other known members of the genus, comprising two previously described species from the same burrow system (*D. yoyo*, *D. troglodytes*) and the type species, *D. maoria*, from New Zealand. Key characters defining this genus (hinge morphology, flower-like organs, "hanging foot" structure) are discussed, especially with regard to their presence in other galeommatoid genera. Intraspecific interaction resembling mating behavior is noted and discussed as one of the few possible examples in the Bivalvia.

Key words: *Divariscintilla*, Galeommatoida, Bivalvia, systematics, anatomy, mating behavior, commensalism, Stomatopoda.

### INTRODUCTION

Investigation of the organisms associated with the sand-burrowing mantis shrimp *Lysiosquilla scabricauda* (Lamarck, 1818) (Crustacea: Stomatopoda: Lysiosquillidae) in shallow waters of eastern Florida has revealed a community of seven molluscan species that appear highly dependent on this specialized habitat. Remarkably, all of these species were found to be either poorly known or undescribed. Accounts of the two species of vitrinellid gastropods—*Cyclostremiscus beaulti* (Fischer, 1857) and *Circulus texanus* (Moore, 1965); Bieler & Mikkelsen, 1988—and two of the five species of bivalves—*Divariscintilla yoyo* Mikkelsen & Bieler, 1989, and *D. troglodytes* Mikkelsen & Bieler, 1989—have appeared elsewhere. This report deals with the remaining three species of galeommatoid bivalves. Although superficially different from the two species previously described, and preliminarily treated as members of another genus (as *Scintilla* spp.; Mikkelsen & Bieler, 1989: 192; Eckelbarger et al., 1990), detailed study has revealed their proper placement in *Divariscintilla*, and has shown them to be in fact more similar to the New Zealand type species, *D. maoria* Powell, 1932, than were the two species previously described from Florida stomatopod burrows.

### MATERIAL AND METHODS

*Lysiosquilla* burrows in shallow-water sand flats at several locations on the central eastern Florida coast were sampled using a stainless steel bait pump ("yabby pump") and sieves of 1-2 mm mesh. Sampling depths during extreme low water ranged from less than 0.5 m to supratidal, when the water level lay several centimeters below the level of the sand.

Living clams were maintained in finger bowls of seawater at ambient laboratory conditions (22-25°C), with variable lighting. Water was changed every 1-2 days, and an irregularly-supplied, unmeasured diet of mixed unicellular algae (e.g., *Isochrysis*, *Chlorella*, *Chaetoceras*) was provided. Behavioral studies were aided by video recordings taken of the living animals in aquaria using a standard commercial 1/2-inch-format video camera equipped with a macro lens.

Transfer of specimens between laboratory bowls was best accomplished using small spoons. The spoon could be applied against the glass from below the specimen to gently break the byssus threads while also cradling the clam. Handling these kinds of animals with forceps is awkward and frequently causes damage to fragile shells and tissue.

Relaxation prior to dissection or preservation was most effectively accomplished with

<sup>1</sup>Harbor Branch Oceanographic Museum, Harbor Branch Oceanographic Institution, 5600 Old Dixie Highway, Ft. Pierce, Florida 34946 U.S.A., and Department of Biological Sciences, Florida Institute of Technology, Melbourne, Florida 32901 U.S.A.

<sup>2</sup>Department of Zoology, Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605 U.S.A.

crystalline magnesium sulfate, added directly to the finger-bowl water in unquantified small amounts. Methylene-blue/basic-fuchsin and neutral red were used to delineate tissues and organs in gross dissections.

For histological serial sections, animals were fixed in 5% buffered formalin (Humason, 1962: 14). Shells were decalcified using either dilute (approximately 0.5%) hydrochloric acid (complete decalcification within minutes) or a 1% solution of ethylenediamine tetraacetic acid (EDTA, adjusted to pH 7.2; decalcification complete in 5-6 days). Specimens were embedded in paraplast, sectioned at 8  $\mu$ m and stained with Gomori's green trichrome (modified from Vacca, 1985). Staining reactions described in the text refer to this method. Colors referred to in the text are supplied for future use, that is, to infer homologies of the various glands. Photomicrographs of sections were taken with an Olympus BH-2 stereomicroscope fitted with an Olympus OM-2 camera with Kodak Panatomic-X (ASA 32) film.

For scanning electron microscopy (SEM), preserved specimens were passed through an ethanol-to-acetone series and critical-point dried. These and air-dried shells were coated with gold/palladium and examined using a Zeiss Novascan-30 scanning electron microscope.

All cited anatomical measurements were taken from specimens of average size (see under descriptions). Throughout the text, "relaxed" refers to the condition of an animal in normal crawling posture and does not refer to any chemical treatment.

Cited institutions are (\* indicates location of type and other voucher material):

- AMNH— American Museum of Natural History, New York, New York  
 DMNH— Delaware Museum of Natural History, Wilmington  
 \*FMNH— Field Museum of Natural History, Chicago, Illinois  
 HBOI— Harbor Branch Oceanographic Institution, Ft. Pierce, Florida  
 \*HBOM— Harbor Branch Oceanographic Museum [formerly Indian River Coastal Zone Museum], HBOI  
 \*MCZ— Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts  
 \*SBMNH— Santa Barbara Museum of Natural History, California  
 SMSLP— Smithsonian Marine Station at Link Port, Ft. Pierce, Florida

\*USNM— National Museum of Natural History, Smithsonian Institution, Washington, D. C.

TAXONOMIC DESCRIPTIONS  
 Family GALEOMMATIDAE Gray, 1840  
 Genus *Divariscintilla* Powell, 1932

Type species: *Divariscintilla maoria* Powell, 1932: 66; by original designation. Recent, New Zealand.

Remarks: Redescribed by Mikkelsen & Bieler (1989: 193). See remarks concerning generic placement under Discussion.

*Divariscintilla octotentaculata* n. sp.  
 (Figs. 1, 4, 7-13, 23, 33)

Material examined

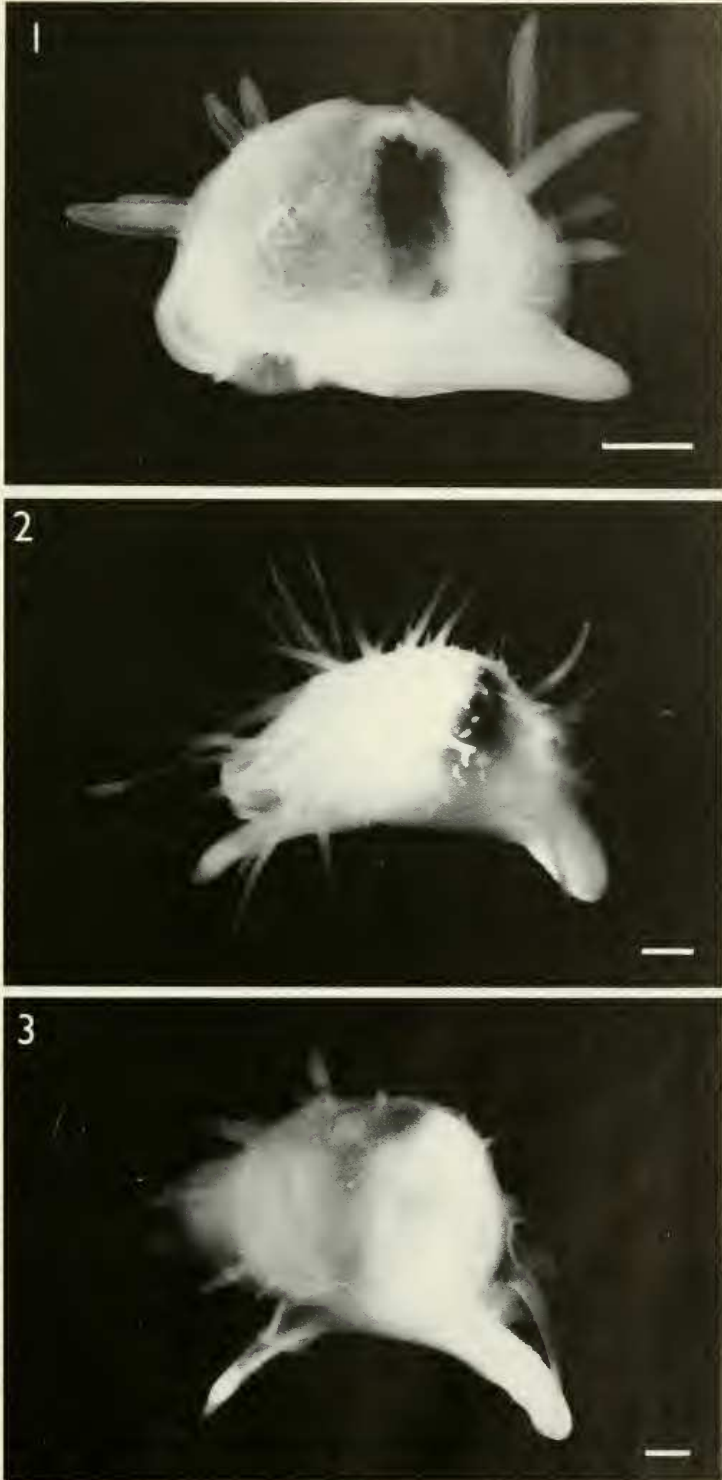
Holotype: 5.3 mm [shell length], FMNH 223401. Paratypes (31): 4.2, 4.2 mm, FMNH 223402; 3.2, 3.2, 3.2, 3.3, 3.3, 3.6, 3.8 mm, HBOM 064:01866; 4.2, 4.2, 3.6, 2.9 mm (preserved soft-bodies + shells coated for SEM), HBOM 064:01867; 3.9, 4.3, 4.3 mm, HBOM 064:01865; 3.0, 3.1, 3.2, 3.4, 3.6 mm, USNM 859443; 3.2, 3.2, 3.2, 3.4, 4.1 mm, MCZ 302510; 1.7, 3.4, 3.4, 3.8, 3.8 mm, SBMNH 35167. Total material: 262 specimens: FLORIDA: Ft. Pierce Inlet: 10 March 1987, 3; 2-3 May 1987, 73; 24 June 1987, 91; 03 August 1987, 2; 14 August 1987, 10; 31 August 1987, 1; 28 December 1987, 7; 11 March 1988, 7; 12 April 1988, 38; 16 October 1990, 2; 03 February 1991, 13. -Sebastian Inlet: 30 December 1987, 26. -St. Lucie Inlet: 18 February 1982, 2.

Type locality

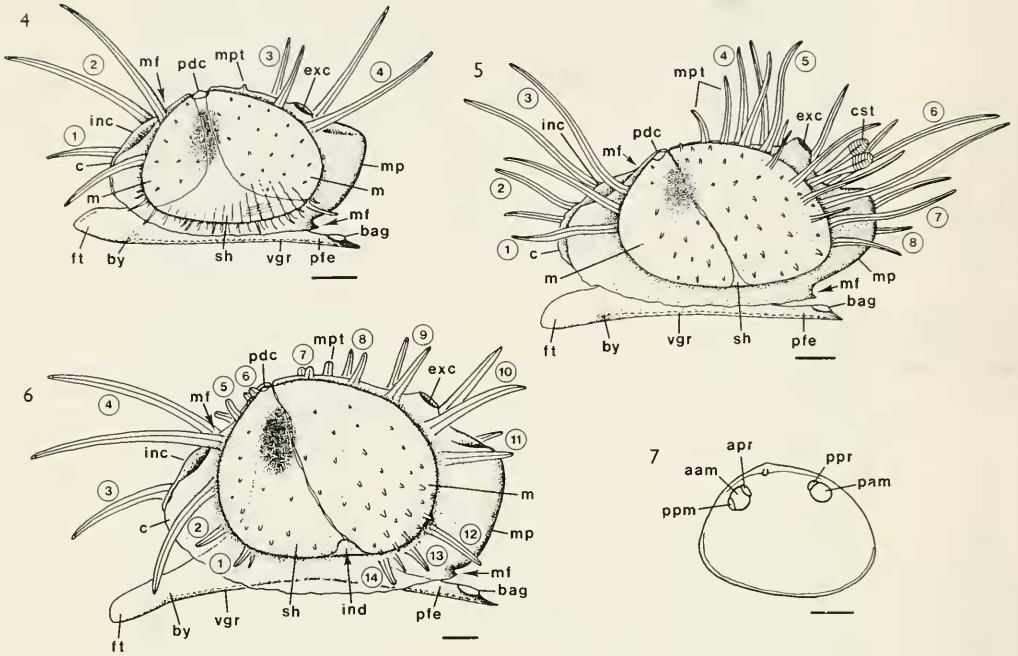
Ft. Pierce Inlet, Indian River Lagoon, St. Lucie County, eastern Florida, 27°28.3'N, 80°17.9'W, occupying *Lysiosquilla scabricauda* burrows on intertidal sand flats with patches of the seagrass *Halodule wrightii* Ascherson. Paratypes all from type locality.

Diagnosis

Animal translucent white. Mantle thin, with retractable, papillose folds covering anterior and posterior thirds of shell. Tentacles originating at dorsal shell margin, two pairs anteriorly, two pairs posteriorly. Posterior foot-extension relatively short. Shell roundly



FIGS. 1-3. Photographs of living animals. 1. *Divariscintilla octotentaculata*. 2. *D. luteocrinita*. 3. *D. cordiformis*. Scale bars = 1.0 mm.



FIGS. 4-7. External appearance and internal shell morphology. Tentacle pairs numbered from anterior to posterior (for text reference only; identical numbers do not imply homology). 4. *Divariscintilla octotentaculata*, in crawling position, from left side. 5. *D. luteocrinita*, same as Fig. 4. 6. *D. cordiformis*, same as Fig. 4. 7. *D. octotentaculata*, internal surface of right valve, showing approximate locations of muscle insertions. Scale bars = 1.0 mm. (aam, anterior adductor muscle scar; apr, anterior pedal retractor muscle scar; bag, byssus adhesive gland; by, location of byssus gland; c, cowl; cst, club-shaped tentacles; exc, excurrent "siphon"; ft, foot; inc, incurrent "siphon"; ind, shell indentation; m, mantle fold; mf, point of mantle fusion; mp, mantle pouch; mpt, median pallial tentacle; pam, posterior adductor muscle scar; pdc, prodissoconch; pfe, posterior foot-extension; ppm, pedal protractor muscle scar; ppr, posterior pedal retractor muscle scar; sh, shell; vgr, ventral pedal groove).

triangular, with umbo slightly anterior, smooth exteriorly, with weak radial ribs interiorly; length approximately 70% of extended mantle length. No "flower-like organ" on anterior surface of visceral mass.

#### Description

**External Features and Mantle:** Living extended animal (Figs. 1, 4) generally 5-7 mm in length, translucent white except for dark digestive gland within visceral mass. Shell largely external, with only anterior and posterior thirds of shell covered in life by mantle folds (Fig. 4, m), not meeting at lateral mid-line. Mantle folds fully retractable, finely papillose, with scattered larger papillae. Mantle thin, extending beyond shell edges; entire surface finely papillose, with fringe of longer

papillae along ventral margin of shell. Two pallial openings: (1) anteropodal opening, from a point anterior to umbones to a point posterior to foot (Fig. 4, mf), forming extensive anterior cowl (Fig. 4, c), the edges of which are held together to form an effective incurrent "siphon" (Fig. 4, inc); and (2) posterodorsal excurrent opening (Fig. 4, exc) between posterior tentacle pairs, either as simple opening or on rounded protuberance forming distinct siphon; appearance dependent on degree of pallial expansion. Posterior mantle fusion forming a rounded, protruding pouch (Fig. 4, mp) containing the gills. Two pairs (one long, one short) retractable, anterior tentacles arising from near shell edge; dorsalmost pair longest. Two pairs (one long, one short) retractable tentacles in vicinity of excurrent siphon, also arising from near shell edge; posteriormost pair longest. A single,

short, mid-dorsal tentacle (Fig. 4, mpt), just posterior to umbo. An additional 1-2 pairs of short tentacles (=enlarged papillae?) in larger specimens (approximately 5 mm) at ventral shell edge at anterior and posterior ends of ventral papillose fringe. Each tentacle with papillose surface and central core of longitudinal muscle and nerve fibers, visible as an inner "thread" under low magnification. Inner pallial fold of non-shell areas (e.g., cowl, ventral mantle margin, posterior pouch) highly muscular.

Preserved specimens completely (or nearly so) retracted into shell, however, shell usually gaping, with tentacles (especially anterodorsal) slightly protruding beyond shell edges.

*Shell* (Figs. 7-11, 13): Shell generally 3-5 mm in length, roundly triangular, longer posteriorly, equivalve, rather compressed, glossy, iridescent, transparent, smooth except for fine concentric growth lines and weak radial ribs most evident interiorly at ventral margin (Fig. 9). Size large relative to mantle, comprising approximately 70% of extended mantle length. Valves held open at a 50-60x angle while crawling, capable of complete closure ventrally but gaping slightly anteriorly and posteriorly. Adductor muscle scars faint, subequal (Figs. 7, 9). Pallial line entire, indistinct. Periostracum colorless, most evident at ventral shell edge (Fig. 9, per).

Hinge line short (Fig. 10). One small, rounded cardinal tooth (Fig. 10, car) in each valve, that of left valve sometimes slightly bifid; lateral teeth absent. Cardinal teeth abutting, not interlocking. External ligament (Fig. 10, lig) weak, amphidetic, supported by nymph. Internal ligament (resilium; Fig. 10, res) stronger, opisthodetic.

Prodissoconch (Fig. 11) brownish-yellow, approximately 360 fm in length. Prodissoconch I corresponding in size to shell of newly released larva, approximately 32% of length of prodissoconch II; sculpture not discernible (surface abraded in adult shell). Prodissoconch II sculptured only with coarse and fine concentric growth lines. Prodissoconch I and II stages distinct, demarcated more by change in convexity than by sculpture or growth discontinuity (Fig. 11, single arrow). Demarcation between prodissoconch II and dissoconch abrupt (Figs. 8; 11, double arrow).

Shell microstructure (Fig. 13) cross-lamellar centrally, with thin prismatic layer covering each side, as in *Divariscintilla yoyo* (see Mikkelsen & Bieler, 1989).

*Organs of the Pallial Cavity*: Foot (Fig. 4, ft) as previously described for *Divariscintilla yoyo* (see Mikkelsen & Bieler, 1989), including hatchet-shaped anterior portion, narrowed posterior extension (Fig. 4, pfe), anterior byssus gland (Fig. 4, by), ciliated ventral groove (Fig. 4, vgr) supplied with numerous mucous glands, and terminal byssus adhesive gland (Fig. 4, bag). Byssus gland of undefined structure, staining turquoise in histological sections; byssus adhesive gland of branching lamellar folds, staining purplish-red. One to four byssus threads produced, emanating from extreme posterior tip of foot. Opaque white pigment band (of unknown function) along anterodorsal tip of foot, staining dark purplish-red in sections.

Anterior and posterior adductor muscles subequal, of moderate diameter. Anterior and posterior pedal retractor muscles smaller in diameter, inserting on shell just dorsal and medial to their respective adductor muscle scars. Very small pedal protractor muscle merging with anteroventral edge of anterior adductor muscle just before both attach to shell; inserting into anterior visceral mass just dorsal of labial palps. Muscles leaving very faint attachment scars on shell (Figs. 7, 9).

Overall morphologies of visceral mass, labial palps and ctenidia as in *Divariscintilla yoyo* (see Mikkelsen & Bieler, 1989). Palps with 6-8 lamellae each side. Ctenidia smooth, unpleated (appearing posteriorly loosely pleated in preserved specimens due to contraction). Outer demibranch approximately 50% smaller than inner; both demibranchs ventrally rounded and with both interfilamental and interlamellar connectives. Ciliary currents on palps and ctenidia not verified.

Flower-like organ absent (see Discussion below).

*Digestive System*: Structure of digestive system (mouth, esophagus, stomach, midgut, hindgut, rectum) of same organization as that in *Divariscintilla yoyo* (see Mikkelsen & Bieler, 1989: fig. 28).

*Suprabranchial Chamber*: Arrangement of openings and presence of glandular patches (?hypobranchial glands; Fig. 23, hyp) adjacent to rectum as in *Divariscintilla yoyo* (see Mikkelsen & Bieler, 1989: fig. 29).

*Nervous System*: Arrangement of ganglia, statocysts, and major nerves as described for *Divariscintilla yoyo* (see Mikkelsen & Bieler, 1989: fig. 31). Left and right posterior tenta-

cles innervated by branches from the pallial nerve, adjacent to its junction with the visceral ganglion. Anterior tentacles similarly innervated but both from a common branch of the pallial nerve, adjacent to its junction with the cerebro-pleural ganglion.

**Reproductive System:** Simultaneous hermaphrodite. Ototestis white, encompassing most of volume of visceral mass, as in *Divariscintilla yoyo* (see Mikkelsen & Bieler, 1989).

Mature spermatozoa morphologically indistinguishable from that of *D. yoyo* (see Eckelbarger et al., 1990: figs. 28-29, table 1; *D. octotentaculata* as *Scintilla* sp.), except smaller in relative size. Spermatogenesis fully described by Eckelbarger et al. (1990; as *Scintilla* sp.).

Brooding large number of small larvae for variable period; brooding time for individuals collected with larvae, 9-15 days ( $n = 4$ ); total brooding time from set to release in laboratory, 9, 10, and 12 days ( $n = 3$ ). Larvae held within both demibranchs and in suprabranchial chamber, where they are circulated via pallial expansions and contractions. During brooding, excurrent siphonal opening constricted by sphincter-like muscle, sometimes noted around free end of rectum, allowing digestive processes to continue. Larvae initially white, turning pink with shell development on day 5-7 ( $n = 2$ ); released as straight-hinged "D" larvae with apical flagella, 115-123  $\mu\text{m}$  in shell length ( $\bar{x} = 119 \mu\text{m}$ ,  $n = 40$ ; Fig. 12). Larvae expelled through excurrent siphon via strong contractions of shell and pallial muscles. Adults brooding larvae collected in May, June, December 1987, and March, April 1988; additional adults setting larvae in laboratory in February, May, June 1982 and November 1990; one specimen setting two broods in laboratory, four months apart, with second brood approximately 20% quantity of first. No apparent seasonality.

**Circulatory and Excretory Systems:** As described for *Divariscintilla yoyo* (see Mikkelsen & Bieler, 1989).

#### Distribution and Abundance

Known from three locations, all on intertidal and shallow subtidal sand flats within the Indian River Lagoon, eastern Florida: the type locality, Ft. Pierce Inlet (St. Lucie County, 27°28.3'N, 80°17.9'W), just north of St. Lucie Inlet (Martin County, 27°11.4'N, 80°11.1'W),

and Sebastian Inlet (Brevard County, 27°51.6'N, 80°27.0'W). May be quite numerous; largest number per burrow sample = 74.

#### Etymology

An adjective, *octotentaculatus*, -a, -um, from the Latin *octo* (eight) and the late Latin *tentaculum* (a "feeler"), referring to the eight long mantle tentacles, a diagnostic feature.

#### Remarks

This is the most common of the five *Divariscintilla* species in the *Lysiosquilla* burrows (see Ecology and Behavior).

Prior to the beginning of this study in March 1987, two individuals of this species were encountered, and are presently the only known specimens of any of the Floridian burrow galeommatoids from previous collections. These were collected in a shovel-and-sieve sample from a sand bar in the Indian River Lagoon, north of St. Lucie Inlet, Martin County, Florida, 27°11.4'N, 80°11.1'W, on 18 February 1982. These individuals were maintained in the laboratory for approximately four months, providing material for notes and photographs on behavior, reproduction, and development.

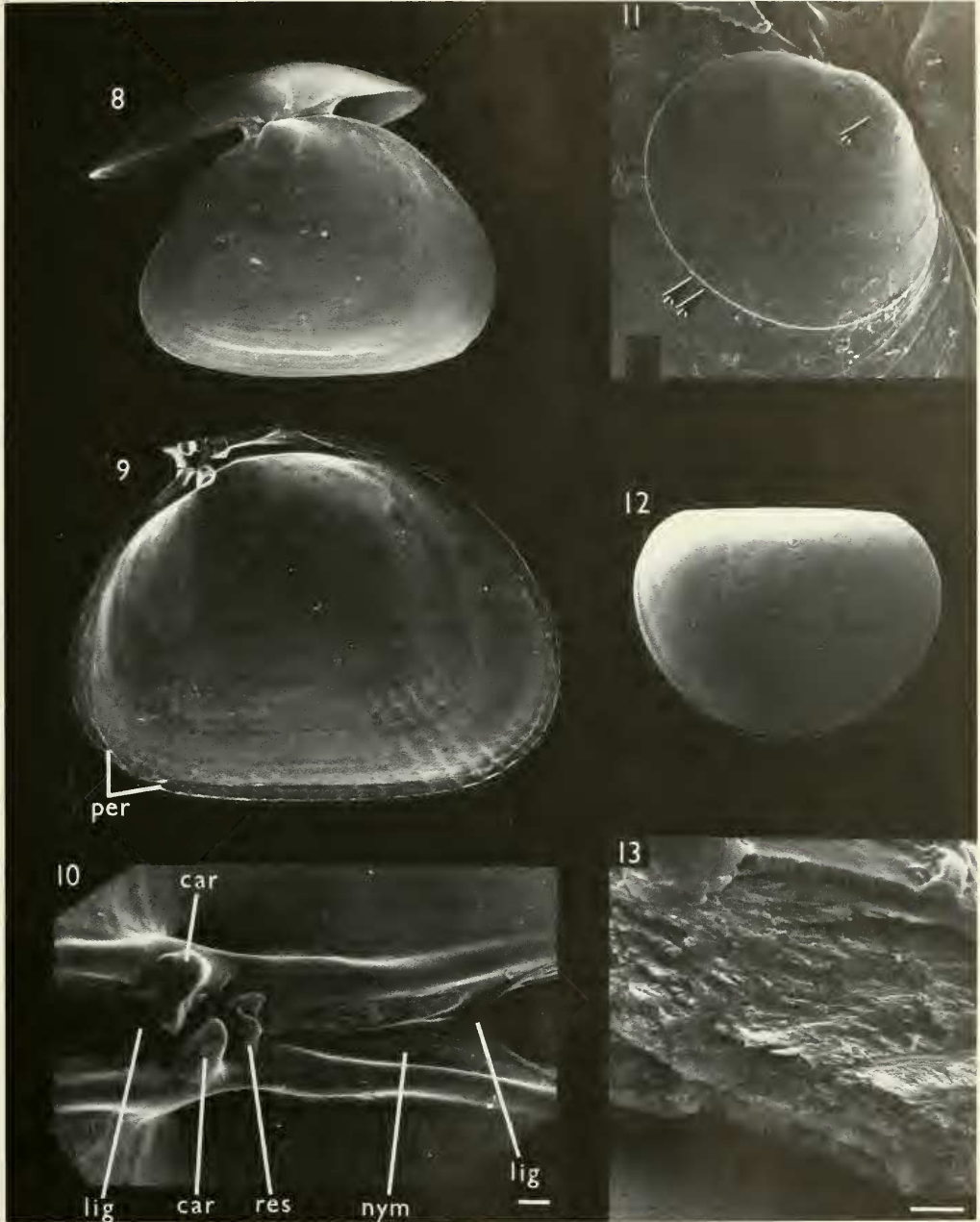
#### *Divariscintilla luteocrinita* n. sp. (Figs. 2, 5, 14-22, 24-25)

#### Material examined

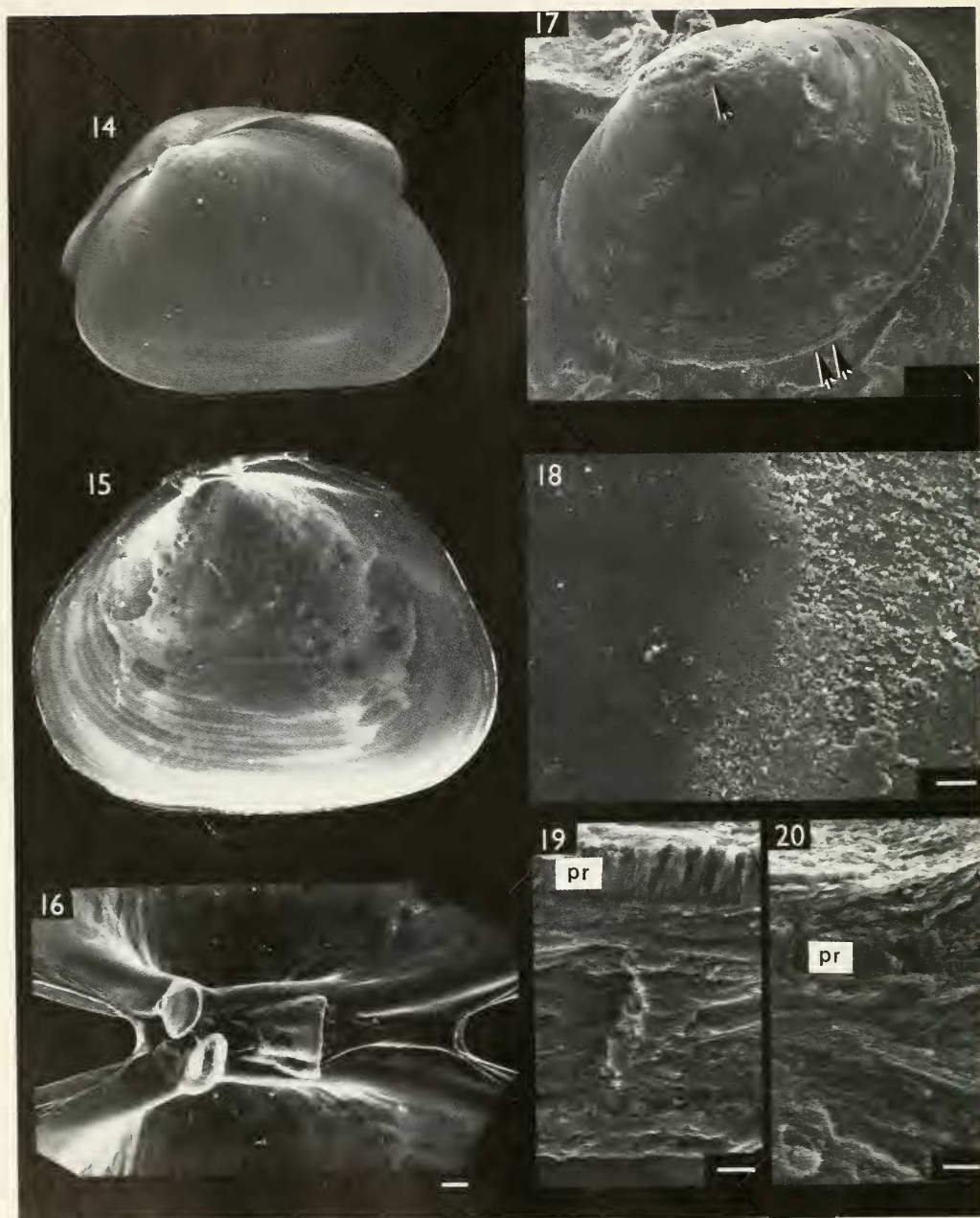
Holotype: 5.0 mm (shell length), FMNH 223403. Paratypes (12): 4.6 mm, FMNH 223407; 4.4 mm (shell only), FMNH 223404; 3.2, 3.9 mm, HBOM 064:01863; 4.9, 4.5, 4.1, 2.9 mm (shells only, coated for SEM), HBOM 064:01864; 4.8 mm, USNM 860195; 5.5 mm (shell only), USNM 859444; 3.4 mm, MCZ 302517; 3.5 mm, SBMNH 35168. Total material: 16 specimens: FLORIDA: Ft. Pierce Inlet: 10 March 1987, 1; 2-3 May 1987, 5; 24 June 1987, 1; 03 August 1987, 1; 14 August 1987, 2; 31 August 1987, 1; 12 April 1988, 1; 03 February 1990; 4.

#### Type locality

Ft. Pierce Inlet, Indian River Lagoon, St. Lucie County, eastern Florida, 27°28.3'N, 80°17.9'W, occupying *Lysiosquilla scabricauda* burrows on intertidal sand flats with



Figs. 8-13. Shell of *Divariscintilla octotentaculata* (SEM). 8. Left valve, external view, 2.9 mm length, paratype, HBOM 064:01867. 9. Right valve, internal view, 3.6 mm length, paratype, HBOM 064:01867. 10. Hinge, anterior to left, paratype, HBOM 064:01867. Scale bar = 100  $\mu$ m. 11. Prodissoconch, 360  $\mu$ m length. Single arrow = prodissoconch I-II boundary. Double arrow = prodissoconch II-dissoconch boundary. 12. Newly released larval shell, 119  $\mu$ m length. 13. Microstructure, with internal surface at top. Scale bar = 5  $\mu$ m. (car, cardinal tooth; lig, external ligament; nym, nymph; per, periostracum; res, resilium).



Figs. 14-20. Shell of *Divariscintilla luteocrinita* (SEM). 14. Left valve, external view, 2.9 mm length, paratype, HBOM 064:01864. 15. Right valve, internal view, 4.9 mm length, paratype, HBOM 064:01864. 16. Hinge, anterior to left, paratype, HBOM 064:01864. Scale bar = 100  $\mu$ m. 17. Prodissoconch, 390  $\mu$ m length. Single arrow = prodissoconch I-II boundary. Double arrow = prodissoconch II-dissoconch boundary. 18. Internal surface, showing smooth adductor muscle scar (left) and adjacent region of opaque thickening (right). Scale bar = 10  $\mu$ m. 19. Microstructure in region of adductor muscle scar; internal surface at top. Scale bar = 5  $\mu$ m. 20. Microstructure in region of opaque thickening, showing additional layer covering internal prismatic layer (pr); internal surface at top. Scale bar = 5  $\mu$ m. (pr, internal prismatic layer).



patches of the seagrass *Halodule wrightii* Ascherson. Paratypes all from type locality.

#### Diagnosis

Animal translucent yellow. Mantle thin, with extensive, retractable, papillose folds completely covering shell, meeting at mid-line. Tentacles originating at shell edge, three pairs anteriorly, two singles and 9-11 pairs posteriorly, plus one pair club-shaped tentacles adjacent to excurrent opening. Posterior foot-extension relatively short. Shell roundly triangular, with umbo slightly anterior, smooth exteriorly, with opaque thickenings interiorly; length approximately 70% of extended mantle length. Single "flower-like organ" on anterior surface of visceral mass.

#### Description

**External Features and Mantle:** Living extended animal (Figs. 2, 5) generally 6-7 mm in length. Mantle and tentacles translucent pale yellow; foot white. Upper portion of digestive gland showing through mantle and shell as dark elongate-oval spot. Shell entirely covered in life by anterior and posterior mantle folds (Fig. 5, m), meeting at lateral dorso-ventral midline on each side. Mantle folds thin, incompletely retractable, entirely finely papillose, with scattered, elongated papillae especially posteroventrally. Mantle edge extending widely beyond shell edges; entire surface finely papillose. Pallial openings, musculature, and posterior pouch as in *Divariscintilla octotentaculata*. Numerous, long, retractile tentacles originating at shell edge: three pairs anterior to umbo; two singles plus five pairs posterior to umbo (= two singles on midline + two pairs + [excurrent siphon] + three pairs). Shorter accessory pairs posterior to umbo originating from mantle fold near, but ventrad of, shell edge: one to three pairs anterior, two to three pairs posterior to excurrent siphon. Structure of these tentacles as in *D. octotentaculata*; those on shell edge adjacent to cowl and posterior pouch (third and sixth, see numbers, Fig. 5) longest. One prominent pair of thicker, whitish, club-shaped tentacles (Fig. 5, cst) immediately posterior to excurrent siphon originating just inside shell edge; internal structure differing slightly from that of other tentacles (see Remarks).

Preserved specimens incompletely retracted into gaping shell; mantle folds contracted to narrow rim along shell edge, expos-

ing most of shell surface; tentacles, cowl, posterior pouch, and foot contracted but still usually extending beyond shell edges.

**Shell** (Figs. 14-20): Shell generally 4-5 mm in length, roundly triangular to oval, longer posteriorly, equivalve, rather inflated, glossy, transparent to translucent white, smooth except for fine concentric growth lines and irregular opaque thickening interiorly, imparting a white-blotched pattern (Fig. 15). Size large relative to mantle, comprising approximately 70% of extended mantle length. Valves held open at approximately 40° angle while crawling, incapable of complete closure. Adductor muscle scars subequal, distinct due to presence of surrounding shell thickening (Fig. 15). Periostracum as in *Divariscintilla octotentaculata*.

Hinge line short (Fig. 16), similar to that of *Divariscintilla octotentaculata*. Both cardinal teeth rounded.

Prodissoconch (Fig. 17) brownish-yellow, approximately 390 μm in length. Prodissoconch I approximately 145 μm in length, approximately 37% of length of prodissoconch II; sculpture not discernible (surface abraded in adult shell). Prodissoconch II sculptured with coarse concentric growth lines. Demarcation between prodissoconch I and II stages (Fig. 17, single arrow), and between prodissoconch II and dissoconch (Figs. 14; 17, double arrow) as in *Divariscintilla octotentaculata*.

Shell microstructure as in *Divariscintilla octotentaculata*, except with additional layer of parallel crystals covering internal perpendicular prismatic layer, forming regions of opaque thickening (Figs. 18-20).

**Organs of the Pallial Cavity:** Foot (Fig. 5, ft) as in *Divariscintilla octotentaculata*. Adductor, pedal retractor, and pedal protractor muscles (including relative positions) as in *D. octotentaculata*. Muscles leaving distinct attachment scars on shell (Fig. 15).

Visceral mass, labial palps and ctenidia as in *Divariscintilla octotentaculata*. Palps with approximately 8 lamellae each side. Outer demibranch approximately 40% smaller than inner. Ciliary currents on palps and ctenidia unknown.

A single "flower-like organ" (Figs. 21-22; see Mikkelsen & Bieler, 1989, for explanation of term) on anterior surface of visceral mass just ventral to labial palps. Size variable, not correlated with shell length.

**Digestive System:** As in *Divariscintilla octotentaculata*.

*Suprabranchial Chamber.* As in *Divariscintilla octotentaculata*, except that the whitish glandular patches (?hypobranchial glands) are much more extensive (Fig. 24).

*Nervous System:* Arrangement of ganglia, statocysts, and major nerves as described for *Divariscintilla yoyo* (see Mikkelsen & Bieler, 1989: fig. 31). Additional tentacular nerves arising (independently) from pallial nerve.

*Reproductive System:* Overall gross morphology as in *Divariscintilla octotentaculata*. Reproductive mode could not be determined from sectioned specimen, which showed no recognizable developed gametes. Adults brooding larvae have not been collected.

*Circulatory and Excretory Systems:* As in *Divariscintilla octotentaculata*.

#### Distribution and Abundance

Known only from the type locality, Ft. Pierce Inlet, St. Lucie County, Florida, 27°28.3'N, 80°17.9'W, on intertidal and shallow subtidal sand flats. Uncommon; only 16 specimens known.

#### Etymology

An adjective, *luteocrinitus*, -a, -um, from the Latin *luteus* (yellow) and the Latin *crinitus* (hairy), referring to the numerous, long, yellowish tentacles, imparting an overall "hairy" appearance.

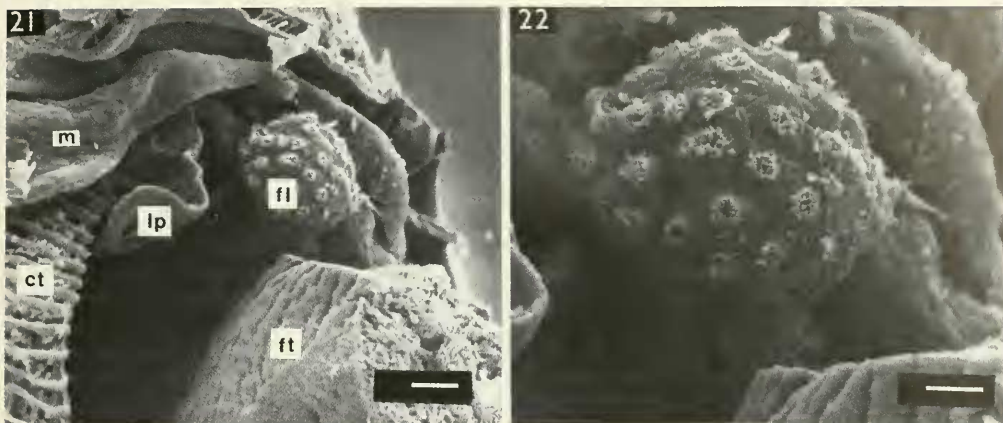
#### Remarks

The single posterior pair of club-shaped tentacles is distinct and consistent in both living and preserved specimens. Normal tentacles (Fig. 25, nt; similar morphology in all five Floridian *Divariscintilla* spp.) show usually four haemocoelic compartments in cross section, each of these supplied with a longitudinal muscle bundle and nerve fiber, and separated by connective tissue septa. The muscle and nerve fibers form a more-or-less concentrated central core, appearing as a central thread under low magnification. Judd (1971: fig. 6) figured a similar internal morphology for tentacles of *Divariscintilla maoria*, but the individual compartmental muscle-plus-nerve bundles are not as concentrated at the core of the tentacle; this difference may not be real, but rather implied by Judd's interpretation of the histological sections. An additional difference

is found in the outer surfaces of the tentacles of *D. luteocrinita*, which are highly papillose and convoluted rather than smooth as in *D. maoria* as shown by Judd (1971: fig. 6). Internally, the club-shaped tentacles of *D. luteocrinita* (Figs. 5, 25, cst) are identical in structure to normal tentacles except that the muscle fibers (Fig. 25, arrow) are dispersed over the surfaces of the septa instead of being concentrated at the core of the tentacle. This difference may allow this particular pair of tentacles to undergo stronger contraction, resulting in the club-like shape. Under full extension, the club shape and whitish coloration of these tentacles disappears, indicating that these features are products of the normally contracted state.

The function of the club-shaped tentacles is unknown. They are probably not homologous to the posterior "defensive appendages" of *D. maoria* (see Judd, 1971: fig. 7) or *Galeomma takii* (Kuroda, 1945) (see B. Morton, 1973a: fig. 5), which can be autotomized and possess only a single, central haemocoelic tube. No tentacles in *D. luteocrinita* have this morphology nor were they ever seen to autotomize. However, these tentacles were often observed to hyperelongate when the animals were disturbed, for example during specimen transfer between laboratory dishes. While most other tentacles contracted, the club-shaped tentacles elongated immediately to 2-3 times the shell length just as the transfer spoon made contact. This bears resemblance to the dymanitic ("threatening") display of tentacles in *Galeomma polita* Deshayes, 1856 (see B. Morton, 1975), and *Ehippodonta oedipus* Morton, 1976 (see B. Morton, 1976), when disturbed, and suggests defensive function. Unlike the dymanitic tentacles of the latter two species, however, the club-shaped tentacles of *D. luteocrinita* do not fully retract into the mantle at rest.

The large "?hypobranchial glands" of this species are located at sites similar to those of the smaller glands of other *Divariscintilla* species, i.e., adjacent to the rectum and the branchial nerves as they join the visceral ganglia. In histological sections, they bear striking resemblance to "seminal receptacles" described and figured for *Aligena elevata* (Stimpson, 1851) by Fox (1979: 101, 103, fig. 32), although in the single sectioned specimen of *D. luteocrinita*, they contained no sperm. The montacutid *Aligena elevata* is a protandrous hermaphrodite, and its seminal receptacles are present only during the fe-



Figs. 21-22. Flower-like organ of *Divariscintilla luteocrinita* (SEM). Anterior tip of foot has been severed to enhance visibility. 21. Scale bar = 100  $\mu\text{m}$ . 22. Scale bar = 50  $\mu\text{m}$ . (ct, ctenidium; fl, flower-like organ; ft, foot; lp, labial palp; m, mantle).

male stage. The occurrence of such structures in Galeommatoidea was summarized by Fox (1979: table 8, as Leptonacea, 15 species), who noted that sperm storage organs were unknown outside of Montacutidae. However, protandry is known in members of other families (e.g. Lasaeidae: *Arthritica crassiformis* Powell, 1933 (see B. Morton, 1973b); see also Fox, 1979: table 11). The reproductive mode of *D. luteocrinita* is presently unknown, but seminal receptacles and/or protandry would be no surprise within the context of this reproductively complex superfamily.

***Divariscintilla cordiformis* n. sp.**  
(Figs. 3, 6, 26-32)

**Material Examined**

Holotype: 5.6 mm (shell length), FMNH 223405. Paratypes (4): 6.4 mm (sectioned on 29 microslides), FMNH 223406; 5.4 mm, HBOM 064:1861; 4.9 mm (partially dissected; prodissoconch coated for SEM), HBOM 064: 01862; 6.4 mm (shell only, coated for SEM), USNM 859445. Total material: 6 specimens: FLORIDA: Ft. Pierce Inlet: 24 June 1987, 2; -Peanut Island: 10 August 1987, 4.

**Type locality**

Peanut Island, near Lake Worth Inlet, Palm Beach County, eastern Florida, 26°46.6'N, 80°02.7'W, occupying *Lysiosquilla scabri-*

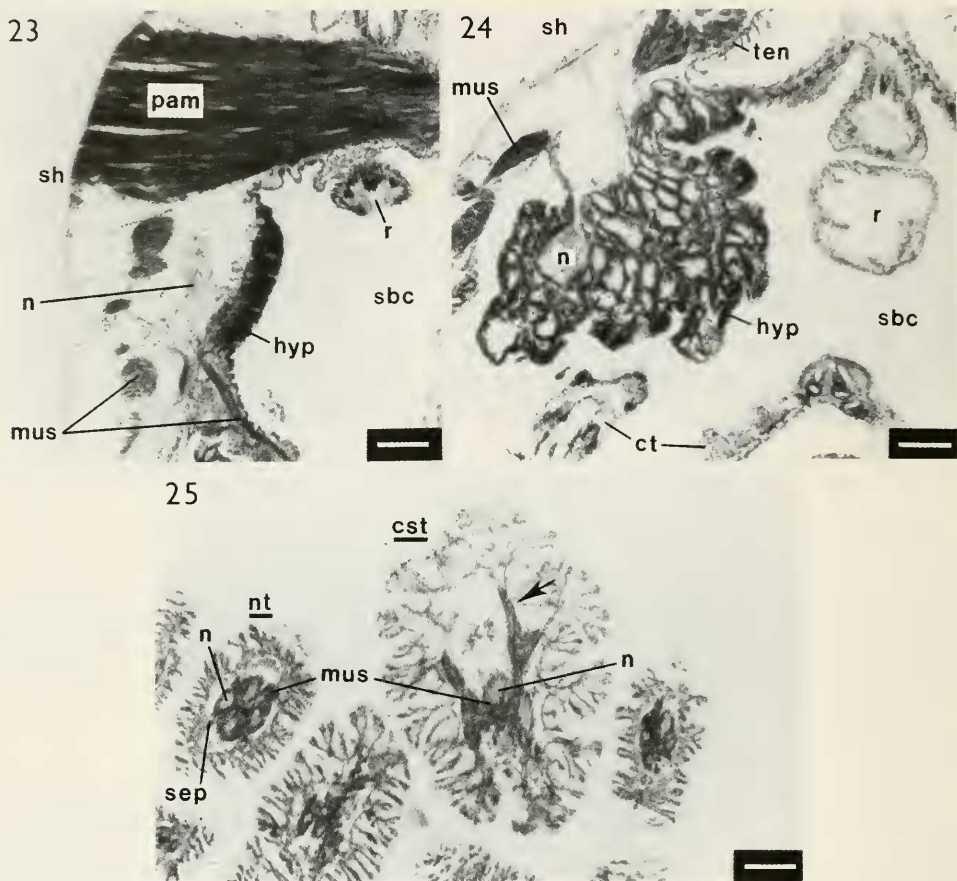
*cauda* burrows on intertidal sand flats with patches of the seagrass *Halodule wrightii* Ascherson. Paratypes from type locality (FMNH, USNM, HBOM 064:01861) or Ft. Pierce Inlet (HBOM 064:01862).

**Diagnosis**

Animal translucent white. Mantle thin, with extensive, retractable papillose folds covering shell completely, meeting at midline. Tentacles originating at shell edge, six pairs anteriorly, eight pairs posteriorly. Posterior foot-extension relatively short. Shell oval, with umbo slightly anterior; length approximately 65% of extended mantle length. Small, ventral, anteriorly directed indentation in each valve. Coarse growth lines and slightly beaded radial ribs restricted to edges of otherwise-smooth shell. Single "flower-like organ" on anterior surface of visceral mass.

**Description**

**External Features and Mantle:** Living extended animal (Figs. 3, 6) generally 7-10 mm in length, translucent white except for dark digestive gland within visceral mass. Shell entirely covered in life by anterior and posterior mantle folds (Fig. 6, m) meeting at lateral dorso-ventral mid-line. Mantle folds thin, incompletely retractable, entirely finely papillose, with scattered larger papillae, which are longest at posteroventral section. Mantle edge extending widely beyond shell edges;



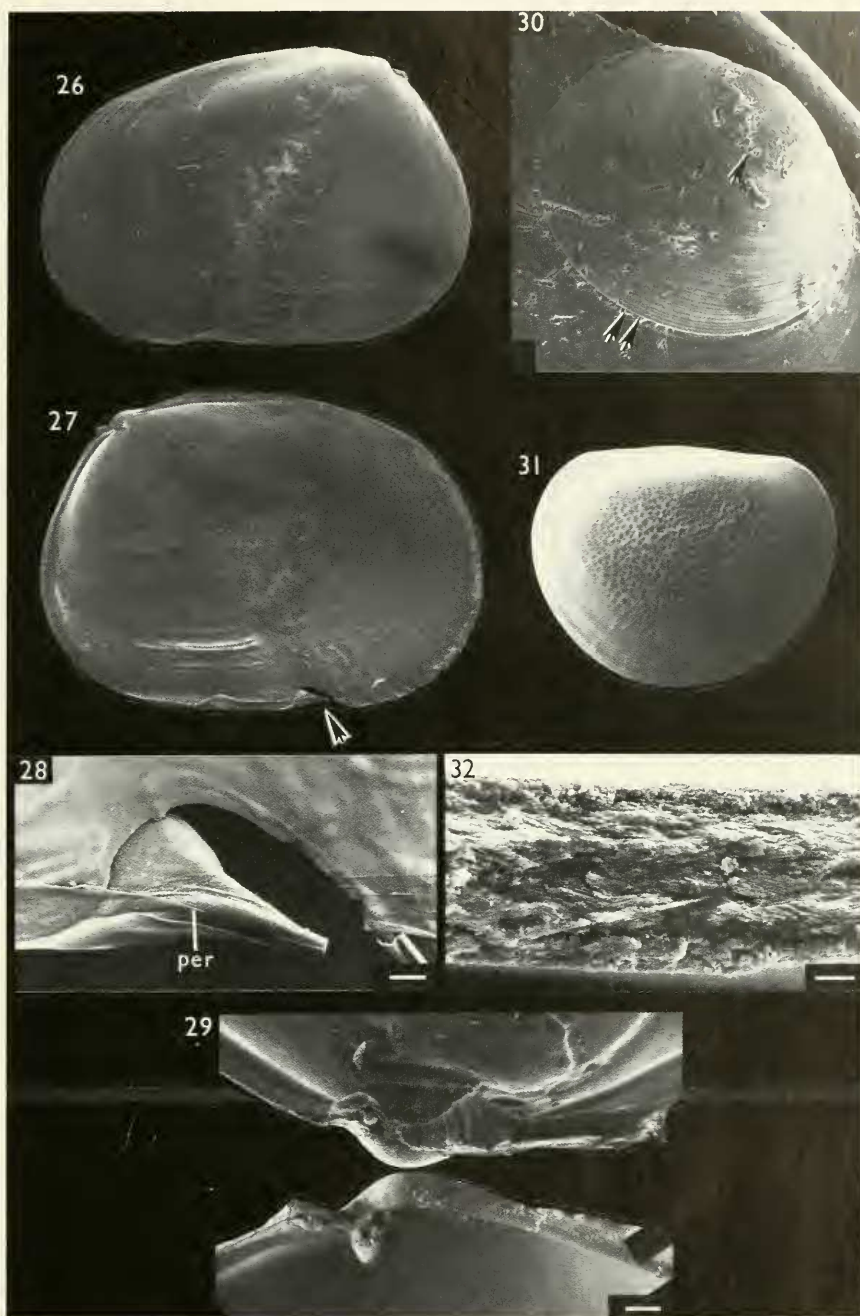
Figs. 23-25. Histological sections. 23. ?Hypobranchial gland adjacent to rectum in *D. octotentaculata*. 24. ?Hypobranchial gland adjacent to rectum in *D. luteocrinita*. 25. Cross-sections of normal and club-shaped tentacles in *D. luteocrinita*. Arrow = muscularized septum. Scale bars = 100  $\mu$ m. (cst, club-shaped tentacle; ct, ctenidium; hyp, ?hypobranchial gland; mus, muscle fibers; n, nerve fiber; nt, normal tentacle; pam, posterior adductor muscle; r, rectum; sbc, suprabranchial chamber; sep, connective tissue septum; sh, shell; ten, tentacle).

entire surface finely papillose, with additional enlarged papillae near shell edge. Ventral mantle edge entire, not cleft in vicinity of ventral shell indentation. Pallial openings, musculature, and posterior pouch as in *Divariscintilla octotentaculata*. Paired, retractable, pallial tentacles numerous, originating near shell edge. Six anterior pairs, those adjacent to cowl area (third and fourth, see numbers, Fig. 6) longest. Eight posterior pairs, those adjacent to excurrent siphon (tenth) longest, but shorter than longest anterior tentacles. A single median tentacle (Fig. 6, mpt) between first and second posterior pairs (Fig. 6, nos. 7, 8). Structure of individual tentacles as in *D.*

*octotentaculata*. Excurrent opening (Fig. 6, exc) between ninth and tenth tentacle pairs.

Preserved animals not fully retracted into gaping shell; mantle folds contracted to narrow rim along shell edge, exposing most of shell surface; tentacles, cowl, and posterior pouch contracted but still usually extending beyond shell edges; foot usually completely withdrawn into pallial cavity.

*Shell* (Figs. 26-30, 32): Shell generally 5-7 mm in length, nearly evenly oval, longer posteriorly, equivalve, compressed, glossy, transparent to translucent white. Small indentation (Figs. 6, ind; 27, arrow; 28) at mid-ventral



Figs. 26-32. Shell of *Divariscintilla cordiformis* (SEM). 26. Right valve, external view, 6.4 mm length, paratype, USNM 859445. 27. Right valve, internal view, 6.4 mm length, paratype, USNM 859445. Arrow = ventral indentation. 28. Close-up of ventral indentation, interior view. Scale bar = 100  $\mu\text{m}$ . 29. Hinge, anterior to left. Scale bar = 200  $\mu\text{m}$ . 30. Prodissoconch, 360  $\mu\text{m}$  length, paratype, HBOM 064:01862. Single arrow = prodissoconch I-II boundary. Double arrow = prodissoconch II-dissoconch boundary. 31. Newly released larval shell, 146  $\mu\text{m}$  length. 32. Microstructure, with internal surface at top. Scale bar = 5  $\mu\text{m}$ . (per, periostracum).

margin, slanting anteriorly toward umbo, evident only on distal 1 mm or so of shell growth (as evidenced by growth lines). Exterior sculpture smooth except for fine concentric growth lines, heavier at anteroventral margin, anterior to indentation. Beaded radial ribs restricted to distal 1 mm or so of shell edge, most prevalent interiorly at posteroventral margin (Fig. 27) and exteriorly at antero- and posterodorsal margins (Fig. 26), forming distinct, fine crenulation at shell edge, absent only at ventral margin immediately anterior to indentation. Size large relative to mantle, comprising approximately 65% of extended mantle length. Valves held open at 20-30° angle while crawling, incapable of complete closure. Adductor muscle scars subequal, faint. Periostracum as in *Divariscintilla octotentaculata*; also evident covering ventral indentation (Fig. 28, per).

Hinge line (Fig. 29) short, as in *Divariscintilla octotentaculata*, with two small rounded cardinal teeth.

Prodissoconch (Fig. 30) brownish-yellow, approximately 360  $\mu\text{m}$  in length. Prodissoconch I corresponding in size to shell of newly released larva, approximately 45% of length of prodissoconch II; sculpture not discernible (surface abraded in adult shell). Prodissoconch II sculptured with coarse concentric growth lines. Demarcation between prodissoconch I and II stages (Fig. 30, single arrow), and between prodissoconch II and dissoconch (Fig. 30, double arrow) as in *Divariscintilla octotentaculata*.

*Organs of the Pallial Cavity:* Foot and shell muscles (adductors, pedal retractors, pedal protractors, including relative positions) as in *Divariscintilla octotentaculata*. Muscles leaving very faint attachment scars on shell (Fig. 27).

Visceral mass, labial palps and ctenidia as in *Divariscintilla octotentaculata*. Palps with approximately seven lamellae each side. Outer demibranch approximately 35% smaller than inner. Ciliary currents on palps and ctenidia unknown.

Single "flower-like organ" (see Mikkelsen & Bieler, 1989) on anterior surface of visceral mass just ventral to labial palps.

*Digestive System:* Similar to that of *Divariscintilla octotentaculata* (relative positions of gastric shield, style sac, digestive diverticula, midgut, etc.), based on histological sections. Limited number of specimens did not permit

confirmation of structure through gross dissection.

*Suprabranchial Chamber:* As in *Divariscintilla octotentaculata*.

*Nervous System:* Arrangement of ganglia, statocysts, and major nerves as described for *Divariscintilla yoyo* (see Mikkelsen & Bieler, 1989: fig. 31). Additional tentacular nerves arising (independently) from pallial nerve.

*Reproductive System:* Simultaneous hermaphrodite. Overall gross morphology as in *Divariscintilla octotentaculata*.

One specimen brooding larvae collected in August 1987. Larvae released one day after collection. Newly-released larval shells 136-148  $\mu\text{m}$  in length ( $\bar{x}$  = 143  $\mu\text{m}$ ,  $n$  = 40; Fig. 31). Adult preserved and subsequently sectioned; apparently intact larvae found in suprabranchial chamber and throughout digestive system, including intestine and rectum (therefore not being digested).

*Circulatory and Excretory Systems:* As in *Divariscintilla octotentaculata*.

#### Distribution and Abundance

Known from the type locality at Peanut Island, Palm Beach County, and from sand flats at Ft. Pierce Inlet, St. Lucie County, Florida, 27°28.3'N, 80°17.9'W. Rare; only 6 specimens known.

#### Etymology

An adjective, *cordiformis*, -e, from the Latin *cordis* (heart) and the Latin *forma* (shape), referring to the ventrally indented shell outline.

#### Remarks

As in *Divariscintilla maoria* (see Judd, 1971), the ventral indentation in the shell of this species does not seem to be functionally important. In both species, it is present in both valves, anteriorly inclined, not developed in juveniles, and not reflected by soft anatomy.

#### ECOLOGY AND BEHAVIOR

As in the two previously described commensal galeommatids (Mikkelsen & Bieler, 1989), no specimens of the newly described species were ever found physically attached

to a mantis shrimp, either in the field or in museum specimens (HBOM). They are assumed to be free-living within the vertical portions of the U-shaped burrow, although specimens were never visible at the opening prior to pumping. Again as with the previous species (Mikkelsen & Bieler, 1989), these clams were never found free-living outside of the burrows or associated with any other burrowing invertebrate in the area (e.g. other mantis shrimps, callianassid shrimps, polychaetes, sipunculans), nor were any empty shells located in dry collections (AMNH, DMNH, FMNH, HBOM, USNM), probably because of their fragile nature.

*Divariscintilla octotentaculata* was the most frequently encountered commensal mollusk in the *Lysiosquilla* burrows; of the 35 burrows containing mollusks, 31 contained *D. octotentaculata*, 20 *D. yoyo*, 19 *D. troglodytes*, 8 *D. luteocrinita*, 6 *Cyclostremiscus beauii*, 7 *Circulus texanus*, and only 2 *D. cordiformis*. *Divariscintilla octotentaculata* was usually collected with other commensals, occurring alone in only 6 of the 31 samples. *Divariscintilla luteocrinita* was always collected with other commensals. *Divariscintilla cordiformis* was collected once with *D. octotentaculata*, and once alone. Densities of *D. octotentaculata* varied greatly, ranging from 1-74 per sample ( $x = 8.3$ ,  $n = 31$ ). *Divariscintilla luteocrinita* was usually present in numbers of only one or two specimens per burrow; one sample contained four specimens. *Divariscintilla cordiformis* was encountered only twice, once as two specimens, once as four. Only a small number of burrows sampled contained commensals. And, as previously reported (Mikkelsen & Bieler, 1989), it must be emphasized that in no case could an entire burrow be sampled using the yabby pump, which only effectively samples its own length (0.5-1.0 m) of the vertical parts of the U-shaped burrow. Estimates of occurrence and/or density of any clams living in the deeper horizontal section of the burrow was thus not possible.

Animals of all three species spent most of their time in the laboratory attached to the glass surface of laboratory bowls by up to four byssus threads, and it is assumed that this is also their habit on the smooth walls of the *Lysiosquilla* burrow. When dislodged, they actively crawl about using an even, gliding motion produced by ciliary action on the central surface of the foot. This was equally effective on the underside of the water surface as on glass. They made no attempts to bur-

row when offered a substrate of loose sand in the laboratory.

All three *Divariscintilla* species previously described (*D. maoria*, Judd, 1971: fig. 4; *D. yoyo* and *D. troglodytes*, Mikkelsen & Bieler, 1989: fig. 32) are known to "hang" from a vertical substrate by the posterior foot-extension, which in these species is extremely long and elastic; byssus threads secreted by the anteriorly located byssus gland are laid down within the ventral groove of the foot and emerge from the terminus to attach to the substrate. The threads are secured within the groove by secretions of the posteriorly located byssus adhesive gland. Byssus and byssus adhesive glands of similar morphologies are present in each of the three new species described here and are assumed to function in the same way. This has been confirmed for *D. octotentaculata* and *D. luteocrinita*, in which secretion of byssus threads, accompanied by distinct pulsing of the byssus gland area, was observed as described for *D. yoyo* and *D. troglodytes* (Mikkelsen & Bieler, 1989). Following this activity, the clam hangs from the posterior foot-extension, with the byssus threads emerging from the posterior terminus of the foot in the vicinity of the byssus adhesive gland. The posterior foot-extension of these species, as well as of *D. cordiformis*, is not as elongated and extensible as in those previously described, therefore the distinctive "hanging" posture, wherein the clam "dangles" from an elongated foot, is not as pronounced.<sup>3</sup>

A peculiar interaction between pairs of *Divariscintilla* species was observed in the laboratory on three occasions. In two instances involving *D. octotentaculata*, one animal of a pair was noted reaching its foot into the mantle cavity of the second specimen, either from in front of or behind its partner. On one of these occasions, the two individuals performed this activity simultaneously, "facing" one another, with each one reaching around the visceral mass of the other to contact the posterior surface with the tip of its foot (Fig. 33). Two specimens of *D. yoyo* have been

<sup>3</sup>Careful notes were not recorded on the behavior of *D. cordiformis* in the early phase of the study, and the inavailability of additional living specimens prevented confirmation of the presence or absence of "hanging" behavior. Morphology suggests that this behavior does occur, however, the shorter posterior extension and the absence of any mention in our preliminary written observations indicates that the "hanging" posture was inconspicuous, as in *D. octotentaculata* and *D. luteocrinita*.

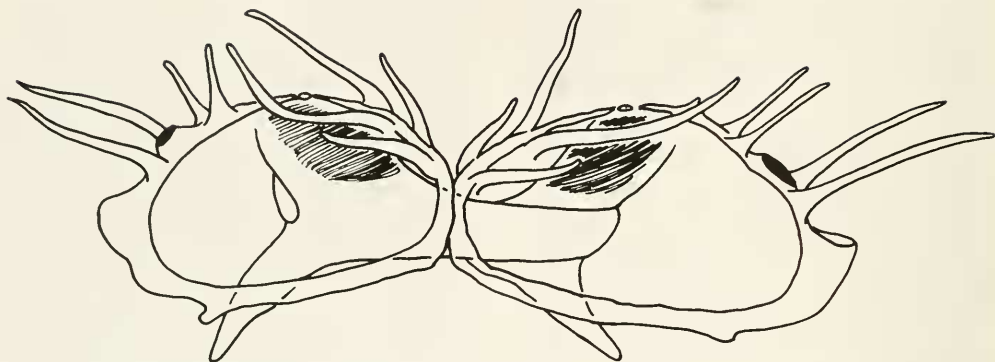


Fig. 33. Mating (?) behavior between two specimens of *Divariscintilla octotentaculata*, as observed in laboratory.

noted performing this same type of activity. In all three instances, the interaction was initiated by the smaller of the two specimens of the pair, and the activity was sustained for 3-7 minutes. Although there is no direct evidence, it seems likely that this observed interaction is part of some sort of reproductive activity, perhaps stimulation of sperm transfer (external gonadal openings are located on the posterodorsal surface of the visceral mass). Each of the two specimens involved in the simultaneous behavior described above had larvae in their suprabranchial chambers within three weeks of the noted activity. (If this behavior is in fact copulatory in function, then this confirms simultaneous hermaphroditism in these species.)

Observed animals of these *Divariscintilla* species do not respond to changes in light intensity (e.g. photographic strobes) and did not seek darkness when offered "artificial burrows" (in the form of black plastic tubes) in the laboratory.

## DISCUSSION

### Generic Placement

The genus *Divariscintilla* was redescribed in a previous part of this study on *Lysiosquilla*-associated mollusks (Mikkelsen & Bieler, 1989). Major emphasis was placed on two features, the presence of flower-like organs and a bipartite foot with both byssus and byssus-adhesive glands, shared between these species and the type species, *D. maoria* Powell, 1932 (the latter described by Judd, 1971).

We regarded the presence of an apparently functionless (Judd, 1971) shell notch in *D. maoria*, as well as the difference in degree of shell coverage by the mantle, as species-level rather than generic characters. At the time, we also considered placement of *D. yoyo* and *D. troglodytes* in the monotypic genus *Phlyctaenachlamys* Popham, 1939, based on *P. lysiosquillina* Popham, 1939. However, there are a number of anatomical characters that distinguish the *Divariscintilla* species (flower organs, hindgut typhlosole, interlamellar ctenidial junctions, relative size of adductor muscles, hinge teeth; compare data of Popham, 1939, and Mikkelsen & Bieler, 1989).

*Divariscintilla luteocrinita* and *D. cordiformis* fit well within *Divariscintilla*, as redescribed. In fact, these new species actually bridge several morphological gaps between *D. maoria* and *D. yoyo/D. troglodytes*, that is shell notch, posterior shell prolongation, less shell internalization, and more numerous posterior tentacles. *Divariscintilla octotentaculata* does not possess the flower-like organs; however, in all other taxonomic characters (hinge, mantle, ctenidia, etc.), it does conform to the redefined genus. The hinge teeth of this species, comprised (as in other *Divariscintilla* species) of only one small cardinal tooth in each valve, was an important element in deciding generic placement. Hinge structure is presently considered taxonomically important at the generic level in Galeommatoidea (P. H. Scott, in litt., October 1990). Most members of the superfamily possess more than one cardinal tooth in at least one valve; some show distinct lateral teeth as well. The genus *Scin-*



TABLE 1. Distinguishing characteristics of all described species of *Divariscintilla*: an expansion of table 1 from Mikkelsen & Bieler (1989).

	<i>D. maoria</i> (from Judd, 1971)	<i>D. yoyo</i>	<i>D.</i> <i>troglodytes</i>	<i>D.</i> <i>octotentaculata</i>	<i>D.</i> <i>luteocrinita</i>	<i>D.</i> <i>cordiformis</i>
Shell:						
General shape	oval	elongate- pointed	oval	roundly triangular	roundly triangular	oval
Ventral indentation	present	absent	absent	absent	absent	present
Prolongation	posterior	anterior	anterior	posterior	posterior	posterior
Internal sculpture	unribbed	unribbed	radially ribbed (marginally)	radially ribbed (marginally)	unribbed, with internal thickening	radially ribbed (marginally)
Length relative to extended mantle length	68%	40%	50%	70%	70%	65%
Prodissoconch length ( $\mu\text{m}$ )	"small"	360	380	360	390	360
Mean newly-released larval shell length ( $\mu\text{m}$ )	unknown	132	126	119	unknown	143
Mantle:						
Color, thickness	(not given)	whitish, thick	yellowish, thin	whitish, thin	yellowish, thin	whitish, thin
Extent covering shell	margins only	entire, umbonal foramen	entire, anterior slit	anterior and posterior thirds	entire, midline overlap	entire, midline overlap
Papillae	very small	sparse, very small	numerous, small, evenly- distributed	numerous, small, longer at ventral edge	numerous, small, evenly- distributed	numerous, small, evenly- distributed
Anterior tentacles	2 pairs	1 pair	2 pairs	2 pairs	3 pairs	6 pairs
Posterior tentacles	1 single	1 single	1 single, 1 pair	1 single, 2-3 pairs	2 singles, 5 pairs, + 3-6 pairs accessory, + 1 pair club-shaped	1 single, 8 pairs
Defensive appendages	6-8 present	absent	absent	absent	absent	absent
Pedal protractor muscle insertion relative to anterior adductor muscle	(not given)	dorsal	dorsal	ventral	ventral	ventral
Flower-like organs: number	1	3-7 (usually 5)	1	0	1	1
Labial palps: Lamellae per palp	approx. 9	10-14	14-20	6-8	approx. 8	approx. 7
Ctenidia:	smooth	pleated	pleated	smooth	smooth	smooth?
Geographical range:	New Zealand	eastern Florida	eastern Florida	eastern Florida	eastern Florida	eastern Florida

*tillona* Finlay, 1927, is the only other genus known to us in which members have a single cardinal tooth in each valve. However, mem-

bers of the latter genus are all attached ecto-commensals on echinoderms, and in addition, are distinguished by a highly specialized,

laterally compressed and furrowed foot. Both of these considerations exclude the new species described here. In view of the taxonomic confusion present in this group, we prefer to use an existing genus until a generic revision of this superfamily based on both shell and anatomical characters can be accomplished.

Coney (1990), in a review of "ventrally notched galeommatid genera," assigned *Divariscintilla yoyo* and *D. troglodytes* to the genus *Phlyctaenachlamys*, and reinstated *Divariscintilla* as a monotypic genus. His reasoning revolved around (1) the shell notch, (2) hinge teeth and ligament morphology, (3) shell ultrastructure, (4) mantle tentacles, (5) degree of shell coverage by the mantle, and (6) ctenidial morphology. We disagree with his taxonomic decisions and address these points as follows:

(1) Shell notch: The newly described species *Divariscintilla cordiformis* has an apparently functionless ventral shell notch very similar to that of the type species *D. maoria*, and agrees well anatomically with the "unnotched" species assigned to *Divariscintilla*. Importantly, the notch does not influence mantle or other soft-part morphology.

(2) Hinge and ligament: Coney (1990: 131, 135) offered conflicting statements regarding hinge teeth. His table of generic characters and description of *Divariscintilla maoria* stated that there was one cardinal tooth in the right valve, whereas his generic description indicated two. Although his scanning photomicrograph of the right hinge (Coney, 1990: fig. 11) seemed on first examination to reveal two cardinal teeth, comparison with our photomicrographs as well as Coney's subsequent text indicated that the posteriormost "knob" was actually the resilium, not a second cardinal tooth. Coney (1990) upheld the original interpretation by Powell (1932) that the left valve was edentulous, although his scanning photomicrograph (Coney, 1990: fig. 12) featured a small structure that may correspond to Powell's (1932: 67) "minute and shapeless vestige" of a left cardinal. Additionally, Coney (1990) noted a ridge in the left valve that he called a posterior lateral tooth. All *Divariscintilla* species (by our definition) possess strengthened or thickened hinge lines to varying degrees, but without development into distinct and/or interlocking lateral teeth/lamellae. As we lack relevant ontogenetic data on shell development, we do not wish to infer homology in this instance and

prefer not to call these structures "lateral teeth."

According to Popham (1939: 66, text-fig. 6), the hinge of *Phlyctaenachlamys lysiosquillina* has two discrete cardinal teeth in the right valve, one cardinal in the left, and an interlocking set of posterior laterals. This is distinctly different from the situation in *Divariscintilla yoyo*, *D. troglodytes*, and *D. maoria*.

Ligament morphology in all *Divariscintilla* species (by our definition) consists of an external amphidetic ligament (inappropriately called "periostacal webbing" at one point in our earlier paper; Mikkelsen & Bieler, 1989: 178) supported by a nymph, and an internal opisthodontic resilium. The resilium is also apparently present in *Phlyctaenachlamys lysiosquillina*, but the external ligament was not mentioned by Popham (1939).

In total, these findings do not agree with Coney's (1990: 142) statement that "the hinge teeth and ligament are remarkably similar between the three species [*lysiosquillina*, *yoyo*, *troglodytes*], but are quite different than those of *Divariscintilla maoria*. . . ."

(3) Shell ultrastructure: This feature was also utilized by Coney (1990) in his discussion of distinguishing characteristics of *Divariscintilla* and *Phlyctaenachlamys* species, although he also (1990: 142) admitted that the "shell ultrastructure of *Phlyctaenachlamys lysiosquillina* is unknown". Studies of the three new species described here (Figs. 13, 19-20, 32), as well as a reevaluation of this character in *D. yoyo* and *D. troglodytes* (see Mikkelsen & Bieler, 1989: figs. 11, 15), indicate that both the inner and outer non-cross-lamellar layers may be prismatic rather than "homogenous" as previously labelled by us. Variability in thickness and/or presence of the various layers among individuals and among different locations on a single valve (e.g. extra internal layer in *D. luteocrinita*, see above) has also been noted. A more exacting study using more appropriate methodology (e.g. sections rather than fractions, see Taylor et al., 1973) is necessary before differences at this level should be employed in taxonomic decisions.

(4) Mantle tentacles: Coney (1990: 142) maintained that "number and placement of mantle tentacles and defensive appendages is strongly similar between *Phlyctaenachlamys lysiosquillina* and those of *P. yoyo* and *P. troglodytes*," noting that none of these species possess the numerous posterior defensive tentacles seen in *Divariscintilla maoria*.

The three new species described here in *Divariscintilla* all possess a number of posterior tentacles, albeit none "defensive." The two primary anterior tentacles, also mentioned specifically by Coney (1990: 142) to combine *P. lysiosquillina*, *D. yoyo*, and *D. troglodytes*, are in fact also present in *Divariscintilla maoria*.

(5) Shell coverage: Although there is a distinct difference in the degree of shell coverage by the mantle between the type species and *Divariscintilla yoyo* and *D. troglodytes*, the three newly described species show intermediate conditions. All *Divariscintilla* species (by our definition) show at least some degree of shell exposure, thus differing from the condition in *Phlyctaenachlamys lysiosquillina* ("the shell is completely embedded"; Popham, 1939: 65). A similar range of variability was described for the genus *Ephippodonta* Tate, 1889, by Arakawa (1960: 57), and can also be found in *Entovalva* Völtkow, 1890, *sensu lato*, wherein the genus *Devonia* was distinguished by Winckworth (1930: 14) for a species with incomplete shell coverage.

(6) Ctenidial morphology: Coney (1990: 142) noted that the ctenidia in *Divariscintilla maoria* are smooth, whereas those of *Phlyctaenachlamys lysiosquillina*, *D. yoyo* and *D. troglodytes* have been described as pleated. However, unlike pleated (= plicate) gills in other bivalve groups (e.g. *Pecten*; see Rice, 1897), pleating in these species is not based on structural differences in the filaments (pers. obs.; Popham, 1939: 71). Some degree of "pleating" caused by contraction in preserved specimens has been noted during the present study. An additional ctenidial character separates *P. lysiosquillina* and the five Floridian species of *Divariscintilla*, in that the latter have interlamellar junctions (unknown for New Zealand *D. maoria*).

Comparative characteristics for all six known species of *Divariscintilla* are presented in Table 1. The three new species described here more closely resemble the type species, *D. maoria* (see Judd, 1971: fig. 1), in general morphology than do the other species previously described during this study (*D. yoyo* and *D. troglodytes*, see Mikkelsen & Bieler, 1989: figs. 1, 2). Like *D. maoria*, the three new species have posteriorly prolonged, relatively large shells and smooth ctenidia (differences in percent reduction of the outer demibranch as cited in the text may not be reliable, as they were taken from preserved specimens and were affected by contraction). One species,

*D. octotentaculata*, has a shell that is similarly incompletely covered by the mantle. Another species, *D. cordiformis*, shows a similar ventral indentation that is likewise apparently functionless. These similarities effectively remove most of the dissimilarity between the New Zealand type species and the included eastern Florida species that existed at the completion of the previous paper (Mikkelsen & Bieler, 1989). *Divariscintilla maoria* is the only species in the genus for which detachable defensive papillae have been described.

#### Distribution

The peculiar pattern of geographic distribution of *Divariscintilla* species, with now five members in the western Atlantic and one in New Zealand, is most likely a result of insufficient sampling of burrow fauna. No ecological niche separation between the five sympatric species was recognized, leaving interesting questions for future research.

#### Comparison with Other Genera

*Divariscintilla* was formerly treated as a subgenus of *Vasconiella* Dall, 1899, by Chavan (1969), apparently on the basis of notched shells. However, members of *V. jeffreysiana* (P. Fischer, 1873), type and sole species of the genus, possess a deep indentation only in the comparatively smaller right valve, and importantly, there are modifications in the right mantle and ctenidial tissues corresponding to the notch (Cornet, 1982). This species is also the only other galeommatoidan with a published account of a "flower-like organ" (Table 2). Unfortunately, although recognizably illustrated by Cornet (1982: fig. 5), no details on structure or possible function were provided for the briefly mentioned "rounded tubercle just under the labial palps" (Cornet, 1982: 39). *Vasconiella jeffreysiana* is probably also commensally associated with a mantis shrimp, *Lysiosquilla eusebia* (Risso, 1816) (Table 2; Cornet, 1982). Differences of *Vasconiella* from *Divariscintilla* (i.e. two cardinal teeth in the left valve, lack of a posterior foot-extension, ?lack of ctenidial interlamellar junctions) prevent synonymy of the two genera as currently defined, but clearly, their relationship should be investigated further.

Mention has been made several times above to the relationships of galeommatoidans with certain phyla of host invertebrates (e.g. echinoderms versus stomatopods). Evi-

TABLE 2. Galeommatoidean species, hosts, and occurrences of flower-like organs and hanging foot structure (x = presence; - = absence).

	Host	Flower-like organs	Hanging foot structure	References(s)
<i>Divariscintilla maoria</i> Powell, 1932	<i>Heterosquilla tricarinata</i> (Claus)	x	x	Judd, 1971
<i>D. yoyo</i> Mikkelsen & Bieler, 1989	<i>Lysiosquilla scabricauda</i> (Lamarck)	x	x	Mikkelsen & Bieler, 1989
<i>D. troglodytes</i> Mikkelsen & Bieler, 1989	<i>Lysiosquilla scabricauda</i> (Lamarck)	x	x	Mikkelsen & Bieler, 1989
<i>D. octotentaculata</i> n. sp.	<i>Lysiosquilla scabricauda</i> (Lamarck)	-	x	This study
<i>D. luteocrinita</i> n. sp.	<i>Lysiosquilla scabricauda</i> (Lamarck)	x	x	This study
<i>D. cordiformis</i> n. sp.	<i>Lysiosquilla scabricauda</i> (Lamarck)	x	x	This study
<i>Parabornia squillina</i> Boss, 1965	<i>Lysiosquilla scabricauda</i> (Lamarck)	x	x	Boss, 1965a; this study
<i>Vasconiella jeffreysiana</i> (P. Fischer, 1873)	? <i>L. eusebia</i> (Risso)	x	-	Cornet, 1982
<i>Phlyctaenachlamys lysiosquillina</i> Popham, 1939	<i>L. maculata</i> (Fabricius)	-	x	Popham, 1939
<i>Ceratobornia longipes</i> (Stimpson, 1855)	<i>Callianassa major</i> Say or <i>Upogebia affinis</i> (Say)	-	x	Jeffreys, 1863; Dall, 1899; Norman, 1891; Jenner & McCrary, 1968
<i>C. cema</i> Narchi, 1966	<i>Callianassa major</i> Say	-	x	Narchi, 1966

dence suggests that host specificity applies mainly to those cases where modifications for locomotion and attachment have occurred. Most "generalist" species (*sensu* B. Morton & Scott, 1989; e.g. *Mysella bidentata* (Montagu, 1803), associated with a wide variety of invertebrates [Boss, 1965b]) possess a simple foot structure consisting of a strong crawling portion (similar to the anterior foot of *Divariscintilla* spp.) ending in a bluntly rounded "heel" from which byssus threads emanate (B. Morton & Scott, 1989: fig. 1 [*Lasaea*], figs. 9-10 [*Pseudopythina*]). This is probably the plesiomorphic condition in the superfamily, compared to the more derived states seen in some of the host specialists. For example, the flattened foot of *Scintillona* spp. (J. E. Morton, 1957) may be a modification for laterally applied locomotion among the vertical spines and papillae of echinoderms to which they attach (Dall et al., 1938: 145; Yamamoto & Habe, 1974; Ó Foighil & Gibson, 1984: 75). Also, the sucker-like anterior foot of *Entovalva* (= *Devonia perrieri* (Malard, 1903) (see Anthony, 1916) allows attachment to the smooth, outer body walls and/or inner cloacal

walls (Bruun, 1938) of burrowing holothurians.

An elongate posterior foot-extension for attachment to a smooth vertical substrate is found in three specialist genera: *Divariscintilla*, *Phlyctaenachlamys* Popham, 1939, and *Ceratobornia* Dall, 1899 (Table 2). All species involved are associated with crustaceans that produce smooth-walled burrows in sand (Table 2). Most are believed to live attached to the crustacean burrow walls (*Ceratobornia cema* may also "temporarily" attach to its host (Narchi, 1966); the biology of *C. longipes* is unknown). Although insufficiently studied in *Phlyctaenachlamys* and *Ceratobornia*, all species apparently possess the same "hanging apparatus" comprised of an anterior byssus gland, ventral groove, and posterior byssus adhesive gland (see Popham, 1939: fig. 2, *P. lysiosquillina*, hanging behavior not specifically described; Narchi, 1966: figs. 1, 5, *C. cema*; Dall, 1899: pl. 88, figs. 10-11, 13, *C. longipes*). They also all possess similar general morphologies of the pallial, ctenidial, digestive, circulatory, excretory, and nervous systems (*C. longipes* incompletely known).

TABLE 3. Distinguishing characteristics for the three galeommatoidean genera possessing the "hanging foot." See text for included species and sources of data. [L, left; R, right]

	<i>Divariscintilla</i>	<i>Phlyctaenachlamys</i>	<i>Ceratobornia</i>
Shell internalization	incomplete	complete	incomplete
Hinge:			
Cardinal teeth	1 R, 1 L	2 R, 1 L	2 R, 2 L
Lateral teeth	absent	1 posterior, reduced	1 posterior, reduced
Retraction into shell	yes (1 sp.) no (5 spp.)	no	yes
Adductor muscles	subequal	posterior reduced	subequal
Flower-like organs	present (5 spp.) absent (1 sp.)	absent	absent
Interlamellar ctenidial junctions:	present	absent	absent
Hindgut typhlosole	present	absent	absent
Hypobranchial gland	present?	absent	absent
Supportive chondroid edge in foot	absent	absent	present

The anatomical differences among the three genera that presently prevent their synonymy are listed in Table 3. Until the importance of each of these characters can be reassessed, it is uncertain whether possession of a "hanging foot" reflects convergence or phylogenetic relationship, and the three genera are best treated separately.

Another possible difference between *Divariscintilla* on one hand and *Phlyctaenachlamys* and *Ceratobornia* on the other lies in the mode of reproduction. Members of *Divariscintilla* for which such data are available (*D. yoyo*, *D. troglodytes*, *D. octotentaculata*, *D. cordiformis*) are known to be simultaneous hermaphrodites. From literature data, it seems that *Phlyctaenachlamys lysiosquillina* and *Ceratobornia cema* are forms with separate sexes (Popham, 1939, p. 80: "specimen sectioned was a male"; and Narchi, 1966, p. 521: "sectioned specimen was a female"). However, while simultaneous hermaphroditism can be documented from individuals without observations over extended periods of time, "males" or "females" could belong to forms with consecutive hermaphroditism. Protandrous and protogynous hermaphroditism have both been reported for the superfamily (summarized by Fox, 1979: tab. 11, as Leptonacea).

*Rhamphidonta* Bernard, 1975, represented by the single species *R. retifera* (Dall, 1899), also possesses a bipartite foot but one which is different from that discussed above, both morphologically and functionally. According to Bernard (1975), the foot of *R. retifera* is

anteriorly elongated, with the main enlarged crawling portion located posteriorly. Members of this species are not known to hang; they burrow into sand to avoid illumination, and are apparently free-living. The hinge of *R. retifera* (see Bernard, 1975: fig. 1) is distinctly "montacutid." Close relationship with the three genera discussed above is unlikely.

The mantis shrimp *Lysiosquilla scabri-cauda* also serves as host to *Parabornia squillina* Boss, 1965, a galeommatoidean that attaches to the inner surface of the abdominal sclera of the shrimp (Table 2). *Parabornia squillina* has been collected in the region of this study (Sebastian Inlet, Peanut Island), but has not been collected in burrows containing *Divariscintilla* species. Interestingly, the animal of *P. squillina* also possesses a single "flower-like organ" (pers. obs.), although this was not mentioned in the original species description based on preserved material. (Boss, 1965a: fig. 3 shows an unexplained five-part zig-zag outline for the visceral mass below the gills and labial palps.) Its foot (Boss, 1965a: fig. 3) appears morphologically similar to the "hanging type" described above; a deep ventral groove ends with an opaque white area at the end of a very short posterior extension (pers. obs.). Boss (1965a: 4) interpreted the white area at the end of the foot as the byssus gland (as did Judd [1971] for *D. maoria*, and Narchi [1966] for *Ceratobornia cema*). In view of the byssus adhesive gland described here and previously (Mikkelsen & Bieler, 1989), this organ (which was depicted with internal lamellae by Boss, 1965a: fig. 3)

warrants reinvestigation. If this structure is the primary byssus gland, what is the function of the ventral groove? (Histological study of the structure of the entire foot, and observations of living animals producing byssus threads would resolve this question.) Boss (1965a) placed *Parabornia* in the Erycinidae (Erycininae), in part, because its hinge has two cardinal teeth in each valve and a central resilium. If hinge structure is eventually confirmed as a reliable taxonomic character based on phylogeny of the group, the "hanging foot" and "flower-like organs" would need to be explained as results of evolutionary convergence and/or symplesiomorphies.

### Mating Behavior in Bivalves

The observed "mating" behavior (Fig. 33) between individuals of *Divariscintilla octotentaculata* as well as of *D. yoyo* is of special interest. Mating behavior has not been confirmed for bivalves (Mackie, 1984: 362). Mackie (1984: 363) summarized the reported cases of associations between females and dwarf males in bivalves and concluded that those interactions would qualify as mating behavior if it can be shown that the associations are confined to a breeding period.

True copulatory behavior is absent in bivalves because they lack copulatory organs. However, several authors (Clapp, 1951: 7; Townsley et al., 1966: 49) have observed male terebinthids (*Bankia* spp.) inserting their exhalant siphons into the inhalant siphons of females during sperm release. Purchon (1977: 295), and subsequently Mackie (1984: 362), interpreted this as the use of an intromittant organ, the development of which would be of "great survival value to species ... living in isolated pieces of drift wood (Purchon, 1977: 295). Similarly, quasi-copulatory behavior in *Divariscintilla* would be advantageous for these small bivalves with limited gamete production, living in restricted, relatively isolated populations within the burrows of their hosts. Selective mating in burrows that contain several other congeneric species would guarantee successful fertilization and make conservative use of male gametes. In our previous discussion of flower-like organs, now known from five species of *Divariscintilla*, we (Mikkelsen & Bieler, 1989: 191) speculated that these organs might emit a pheromone for attracting reproductive partners (another possibility, if they are indeed phero-

mone-emitting organs, would be the attraction of larvae to settlement sites).

### ACKNOWLEDGMENTS

The following are gratefully acknowledged: Dr. Raymond B. Manning (USNM), for bringing this interesting fauna to our attention; William D. ("Woody") Lee (SMSLP), for invaluable field help; Paul H. Scott (SBMNH), for comments on generic placement; Patricia A. Linley and Pamela Blades-Eckelbarger (both HBOI) for SEM assistance; Tom Smoyer (HBOI) for photographic work; Dr. Kerry B. Clark (Florida Institute of Technology, Melbourne) and John E. Miller (formerly HBOI) for the use of and help with video recording equipment; Paul S. Mikkelsen (formerly HBOI), for behavioral and developmental notes and the photograph in Fig. 1; Chris Bauman (Vero Beach, Florida) for the illustration in Fig. 33; Paul H. Scott (SBMNH), Dr. Kenneth J. Boss (MCZ), and two anonymous reviewers for valuable comments on the manuscript.

This research was supported in part by the Smithsonian Marine Station at Link Port; the cooperation of Dr. Mary E. Rice and her staff is gratefully acknowledged. Funding for this project was derived in part from a National Capital Shell Club scholarship to P. M., and a NATO Postdoctoral Research Fellowship at SMSLP to R. B. This is Harbor Branch Oceanographic Institution Contribution no. 862 and Smithsonian Marine Station Contribution no. 273.

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Revised Ms accepted 1 August 1991